

AMAZONIANA	VI	2	203 – 235	Kiel, März 1977
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From cooperation between Max Planck Institute for Limnology, Department of Tropical Ecology, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus—Amazonas, Brazil

Da cooperação entre Max-Planck-Institut für Limnologie, Abteilung Tropenökologie, Plön, Alemanha, e Instituto Nacional de Pesquisas da Amazônia, Manaus—Amazonas, Brasil

Qualitative and quantitative investigations on the macrobenthic fauna of Central Amazon lakes.

I. Lago Tupé, a black water lake on the lower Rio Negro.

by

Friedrich Reiss

1. Introduction

The Amazon region with its area of about 7,5 million km² is one of the largest natural landscapes on earth hitherto undisturbed by man. This vast area is covered with rain forest and shows little climatic and spatial differentiation; however, it is possible to divide this apparently uniform area on the basis of the geochemical properties of the soil (FITTKAU 1971 a, b). A central area, characterised by extremely nutrient-poor soils originating from redeposited tertiary to quaternary soils and clays, contrasts sharply with the nutrient-rich Andes foothill zone to the west. The generally nutrient-richer areas of the Guayana-Brazilian Shield abut to the north and south. The northern and southern border areas of the Andean foothills partially surround the nutrient-poor Central Amazon region in the shape of a horse-shoe. The eastern border of the Central Amazon is approximately at Parintins, east of the mouth of the Rio Tapajós (FITTKAU 1975). The Lower Amazon to the east is a relatively small zone between the shields; it differs both from them and the Central Amazon in geomorphology, hydrology and climate rather than in geochemistry. The Central Amazon is divided along the rivers arising in the Andean foothills (e.g. the Rio Solimões, Juruá, Japurá, Madeira) by broad, relatively nutrient-rich stretches of alluvial land. From the edaphic and biological points of view, these areas (called várzea) represent extensions of the Andean foothill zone.

It has been known for some years that the water chemistry of Amazonian rivers and streams indicates the geochemical nature of their upper catchment areas, and on this basis they have been classified as black, white and clear waters (SIOLI 1950, 1951 a, 1957, 1965). Thus rivers with drainage systems in the nutrient-poor Central Amazon have strongly acidic black water poor in electrolytes and with a high content of humic substances, while those

crossing the Andes foothills contain white water richer in electrolytes, and are weakly acidic or alkaline; the turbidity is largely a result of inorganic suspensoids (SCHMIDT 1972 a). These two water types of contrasting properties characterise the Central Amazon.

Clear water rivers such as the Tapajós and the Xingú arise in the Central Brazilian shield; they are neutral to acidic and are made slightly turbid by organic and inorganic material. This water type is of little importance in the Central Amazon.

The rainfall is seasonal so that each year there is a wet and a dry period; as a result, all the large rivers of the Amazon region exhibit water level fluctuations of various magnitude. These can be as great as 20 m (on the upper Rio Solimões) each year, and on the lower Rio Solimões the annual mean is 10,21 m. These fluctuations affect not only the rivers and streams, but also their extensive floodplains (SIOLI 1968) in which standing water bodies can form during high and low water periods. The benthic fauna of these water bodies is the subject of this investigation.

Strictly speaking, the limnological designation "lake" does not apply to these waters. They are normally shallow and in years when the water level of the rivers is particularly low, can dry out wholly or partially; in addition there can be fairly strong currents in them. The term "lake" will, however, be used here. "Várzea lake", meaning the standing waters of the inundated land of the Amazonian white water rivers, is a term well established in the literature, and these waters are often similar to true lakes. They can show persistent thermal stratification and high phytoplanktonic primary production at high water levels (SCHMIDT 1973 a, b). The same is true for the water bodies characterised as black water "lakes" in this paper. The basin morphology of many of them shows that they are fresh water rias (GOUROU 1950), so they can be called ria lakes.

Variations in water quality and quantity with space and time give rise to an extraordinary range of water types, which includes all imaginable intermediates between the three main categories of flowing water, namely white, black and clear waters. The same is true for those standing waters which are almost always in contact with such flowing water; these can in their turn show all the intermediates of the running water systems. It therefore appeared meaningful to investigate the benthic fauna of several lakes in a relatively small area.

One black water lake and six várzea lakes in the vicinity of Manaus, Central Amazon, were chosen for investigation, working on the assumption (discussed later) that várzea lakes are limnologically better differentiated than black water lakes. Since the investigation was restricted to a small part of the Central Amazon, the uniformity of the major external factors, e.g. precipitation, water level fluctuations and sediment load was assured. Also, results obtained from several lakes allows for general conclusions to be drawn, an impossibility when only one lake is sampled, no matter how frequently the data are collected.

An unavoidable disadvantage of such a sampling programme is that the results obtained have limited applicability to the other Amazon regions - the northern and southern border areas, the Andes foothills, and the Lower Amazon. Thus the benthic fauna of the Central Amazon várzea lakes is qualitatively different to, say, that of comparable várzea lakes of the Lower Amazon. It is surely reasonable to assume that limnologically similar standing waters of the Amazon region contain similar species of benthos. Benthic zoocoenoses of different species composition are functionally different. Central Amazon lakes, therefore, cannot really be compared with those of the other Amazon regions until equally extensive qualitative and quantitative data are available for them.

The results of these studies will be presented in three parts; the first deals with the

zoobenthos of the black water Lago Tupé, the second compares six Central Amazon várzea lakes (REISS 1976) and the third will include qualitative and quantitative data on the benthic fauna of Amazonian lakes sampled at random.

The identification of the collected material posed problems since little or no work has been done on many important groups of benthic organisms. For example, of the over 50 species of chironomid and chaoborid larvae encountered in the lakes sampled, none has to date been described. These dipteran groups together account for 53,4 % of the mean annual benthic abundance in all seven lakes (Chironomidae 25,1 %, Chaoboridae 28,3 %).

I would like to thank my colleagues who made species determinations in the following animal groups:

Prof. Dr. J.N. Belkin, Los Angeles	Chaoboridae
Dipl.-Biol. G.O. Brandorff, Plön	Phyllopoda, Copepoda
Dr. D. Hiller, Hamburg	Ostracoda
Dr. C. Meier-Brook, Tübingen	Gastropoda
Dr. V. Puthz, Schlitz	Ephemeroptera
Dr. F. Riemann, Bremerhaven	Nematoda
Dr. D. Stechmann, Kiel	Hydrachnellae
Dr. L. Tiefenbacher, Munich	Decapoda

In particular, I would like to thank Dr. Paulo de Almeida Machado, General Director of INPA at the time, for providing me with a place to work in his Institute during the 1 1/2 years of field work.

My thanks also to Miss G. Konopka, Plön, who did the diagrams, to Mr. Antônio José dos Santos, INPA, Manaus, for help with the field work, and to Miss Louise Glück, Manaus, for laboratory work.

2. The Sampling Area

The seven lakes sampled are in the Brazilian state of Amazonas near the capital city Manaus (Fig.1). As the crow flies, Lago Jacaretinga and Lago Tupé are closest to Manaus (28 km) and Lago Cabaliana is the furthest away (90 km). Lakes 1 to 6 are in the várzea of the lower Rio Solimões (upper Amazon River) and no. 7, the black water Lago Tupé, is on the lower Rio Negro.

The geology of the sampling area is described in a comprehensive paper by FITT-KAU (1974) on the geological development of the Amazon, and need not be given in detail here. It should just be pointed out again that the várzea of the Amazon River and the Rio Solimões is composed of recent almost unleached and therefore fairly nutrient-rich alluvium which exhibits high sedimentation dynamics. In the light of recent results obtained from the Lower Amazon it is possible to say that those sampling areas not influenced by these white water sediments are mainly of pleistocene origin and contain very little tertiary and clay sediment; as a result of frequent deposition under tropical climatic conditions they have been extensively leached and yield soils extremely poor in nutrients.

The Manaus area has a tropical rain forest climate (REINKE 1962) which is of the Amwi type in the Köppen scheme. The short (2 to 3 months) dry season falls in the months

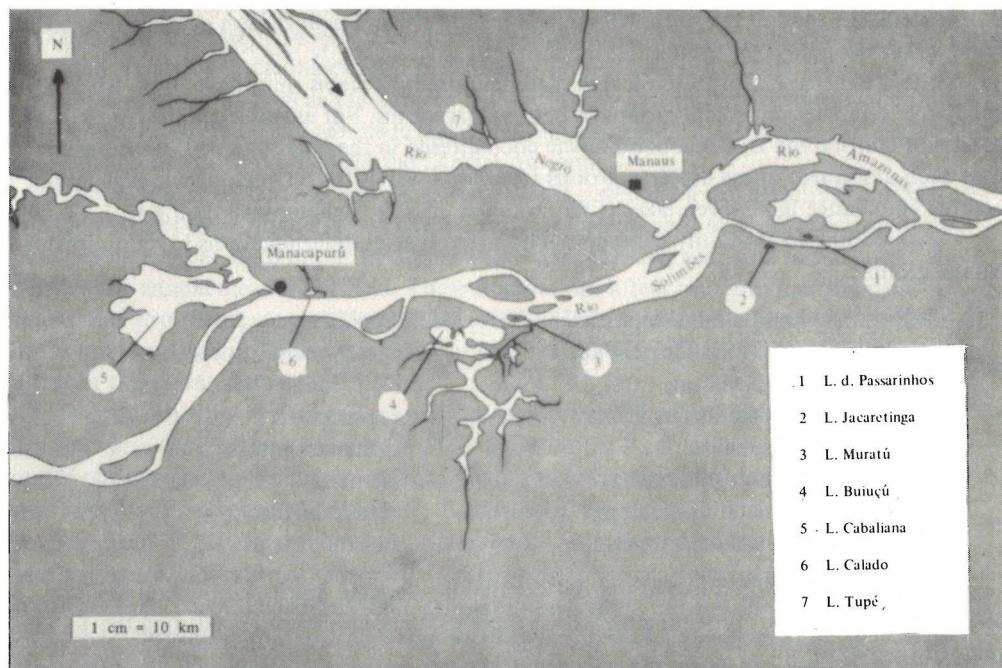


Fig. 1: Location of the seven lakes investigated.

July or August to September, and the rainy season is from January to May, with April usually being the month of maximum rainfall. The mean annual rainfall according to the weather station at Manaus was 2410 mm for the years 1966-1971; however, this as well as the seasonal division of precipitation can vary a great deal from year to year, which influences greatly the hydrography of the water bodies investigated, as will be shown later.

The prevailing winds of the Manaus area are north east to east since the effects of the trade wind can be felt along the Amazon Valley to deep within the South American sub-continent. The thermal stratification of the lakes and therefore, indirectly, their benthic faunal composition are a result of the combined effect of their size, basin morphology and position of the longitudinal axis in relation of the prevailing winds.

The annual rainfall distribution pattern (dry season in the southern winter, rainy season in the summer to autumn) of the catchment areas of the Rio Solimões and the Rio Negro is similar to that of the Manaus area. The resulting annual water level fluctuations determine the hydrography of the water bodies sampled. According to the water gauge at Manaus, the mean annual amplitude for the years 1902 to 1972 was 10.12 m with a maximum of 14.13 m (in 1909) and a minimum of 5.45 m (in 1912). The highest water level is in May-June i.e. about 2 months after maximum rainfall, and the lowest in late October/early December i.e. about 2 months after the period of minimum rainfall. Thus the high and low water periods are slightly displaced in relation to the rainy and dry seasons (see SCHMIDT 1973 a, Fig. 4).

The question of whether the pattern of water level fluctuations of the lower Rio Negro, measured at Manaus, is the same as that of the Amazon-Solimões system in this region is discussed by SCHMIDT (1973 a). He showed that between April and August 1969 the water level curve of the Rio Negro at Manaus ran almost parallel to that of the Lago do Castanho in the várzea of the lower Rio Solimões. Schmidt gives the reason as being that the Rio Solimões, which contains far more water, dams the Rio Negro in the area of the mouth; the water level at Manaus therefore largely reflects the fluctuations of the Rio Solimões.

This assumption was confirmed by the results of daily¹⁾ water level measurements on the lower Rio Solimões, taken over a year (from 13.5.1971 to 10.5.1972) (Fig. 2). The gauge was at the mouth of Lago Calado in the Rio Solimões, on average about 20 m from the shore in the mouth area of the natural canal draining Lago Calado. A comparison of this curve with the one obtained from Manaus shows that the two run largely parallel. In Fig. 2 the maxima of the two gauges have been arbitrarily equated since absolute values for the Rio Solimões are unknown. Thus it appears that the pattern of water level fluctuations of the lower Rio Solimões area is very similar to that measured on the Rio Negro gauge near Manaus.

3. Sampling Period and Methods

All lakes were sampled over a complete year between May 1971 and May 1972, thus allowing studies of qualitative and quantitative seasonal changes in the benthic fauna. Prolongation of the sampling period to cover a further year would have made only marginal differences to the accuracy of the results from the statistical point of view, and this was therefore not done. It is more important in my opinion to consider whether the sampling period itself was a representative year in terms of the external factors determining the annual fluctuations in environmental conditions. The normality or otherwise of the sampling period is best judged by studying the water level curve, the maximum, minimum and amplitude of which are critical in their influence on abiotic and biotic factors in the lakes investigated.

According to the measurements taken on the gauge at Manaus (Fig. 2) the sampling period was distinguished in that the maximum water level of 29.12 m was 1.51 m above the mean maximum of 27.61 m and only 0.58 m below the maximum so far recorded (in 1953). Conditions during the low water period of 1971 were even more extreme; the minimum water level of 21.14 m was only 0.1 m below the highest recorded value of 21.24 m (in 1913), and 3.65 m above the mean minimum level of 17.49 m. The amplitude of water level fluctuation in 1971 was 2.14 m less than the average of 10.12 m. The year 1972, part of which fell in the sampling period, was also a year of very high water with a maximum and minimum of 28.69 m and 20.05 m respectively. The effects of this abnormal hydrological situation on the benthic fauna are discussed under the individual lakes.

Batches of samples were taken from the várzea lakes at intervals of 3 weeks, except for the first two and the last batches when the interval was 2 weeks. Since the benthic fauna in the black water Lago Tupé was so poorly developed it was only necessary to sample here once a month.

In every lake, samples were taken from a fixed station in the middle, which in the shallow basin-shaped Central Amazon lakes was also the position of maximum water depth. Sampling was begun in May, shortly before maximum water level. It was impossible in most lakes to establish a fixed sampling station in the shore region at the same time, since the várzea of the Rio Solimões is completely inundated, except for a few terra firme islands, when the water level is as high as it was in 1971. The shore sampling stations were therefore first established during the low water period in October; the study of qualitative and quantitative changes in the shore zoocoenoses thus does not extend over a full year, except in Lago Cabaliana in which the shore station was selected with the help of the local people during the high water period.

1) Many thanks to Mr. Paulo Krauss for carrying out these daily water level measurements.

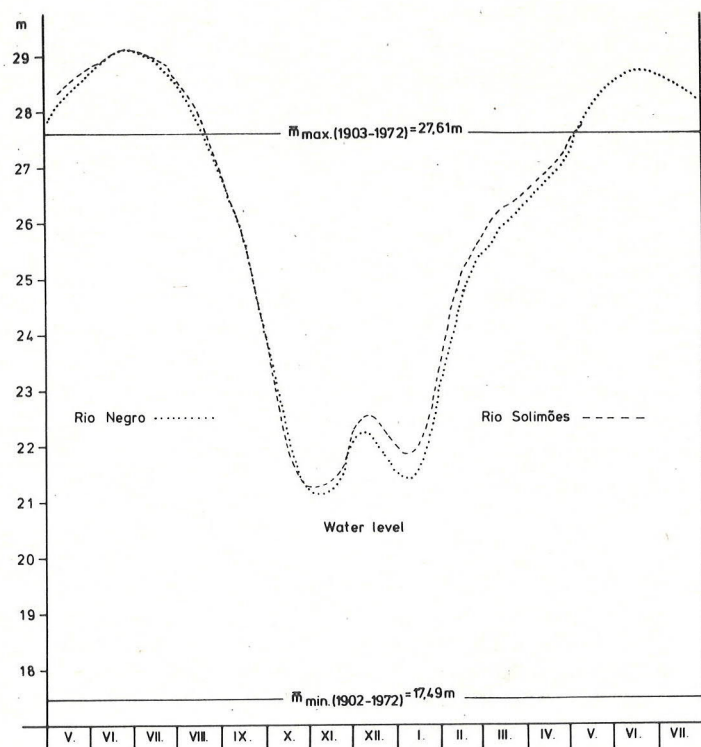


Fig. 2: Water level fluctuations of the lower Rio Negro at Manaus and of the lower Rio Solimões at the mouth of Lago Calado in 1971/72. The mean maximum and minimum water level values at Manaus for a 70 year period are also shown.

At all sampling stations, 3-8 sediment samples were taken using a slightly modified Eckmann-Birge bottom sampler (base 225 cm²), and sieved immediately through a net of 400 μ mesh width. The use of a smaller mesh was impractical since the quantitative extraction of living animals would have been impossible; it was also thought to be unnecessary since most animals are retained in a mesh of 400 μ . The exceptions are the very small Ostracoda and Nematoda. The loss of these groups was calculated as 20-40 % in a 400 μ sieve when compared with a 220 μ sieve.

In addition to this routine programme, sediment samples of the seven lakes were taken from under the floating meadows, along vertical profiles from the shore to the lake middle, and during the phase of rapidly falling water level from sediment which had already dried out. Comparable benthos samples were also taken at random from several other lakes, canals, river courses and small water bodies of the Central and Lower Amazon.

The time lapse between sample taking and field or laboratory analysis varied from a few hours to a maximum of two days. The loss of individual animals during this period due to the presence of carnivorous species in the samples could not be taken into account. The tolerance of the central lake fauna and, to a lesser extent, shore fauna to the high temperatures and unfavourable oxygen conditions during transport to the laboratory was surprisingly high, and dead animals were rarely found. It was shown experimentally that the larvae of, for example, *Chironomus gigas* taken from the deep sediments of the várzea lakes survived for 8 days at 25°C with no visible injury in a sample bottle full of wet sieve material consisting mainly of coarse plant detritus. The larvae of *Campsurus notatus* (Ephemerae) from the same localities could survive similar conditions for 3 days. This is probably because the fauna from

the deeper areas of these Central Amazon lakes is adapted to withstand conditions of oxygen stress under natural conditions.

The animals were fixed in 40% formalin and not later than one week after sampling, divided into groups, blotted dry and weighed. The biomass figures given in this paper are therefore based on wet weight. The molluscs were weight with their shells and the fixing liquid contained inside them. For Nematoda and Ostracoda, 250 individuals were weight and mean weights of 0.05 and 0.08 mg/individual respectively were calculated; these figures enabled calculation of corresponding biomass values. The empty ostracod and mollusc shells found in large numbers in some samples were discarded. Empty trichopteran larval cases similar case-carrying chironomid larvae were also not counted.

According to WINBERG (1971) the wet weight of zoobenthos can be converted to dry weight using the factor 0.2.

The biomass and abundance values given for the 19 sample batches of the sampling period are the means of at least three individual samples; thus the extent of variation can also be given if required. More extensive statistical treatment is impossible because of the small number of samples per batch. A total of 711 sediment samples was taken in all seven lakes, of which 240 came from the shore stations, 457 from the central lake stations, and 14 from other places.

The qualitative composition of the benthic fauna was studied by regularly breeding insect larvae to the adult stage. The rapid fungal infestation of the substrates in the breeding chambers which occurs under tropical conditions can be much reduced by controlling environmental conditions in the laboratory rooms and ventilating the chambers. Breeding periods extending over months are then possible so that those species with a longer development time can be included. Additional information was obtained by taking regular samples of the surface drift and samples of insects in the shore vegetation.

The following abiotic factors were determined on each sampling occasion:

- Secchi transparency with a white Secchi disc of 30 cm diameter.
- Water temperature, with a thermometer mounted in a Van Dorn water sampler.
- pH, using the laboratory meter WTW pH 54.
- Electrical conductivity, using the laboratory meter WTW LF 54 (see SCHMIDT 1972a).
- Oxygen concentrations by the Winkler method.

For the central lake sampling stations, factors (b) to (e) were measured on water samples taken from the surface as well as from about 0.5 m above the lake bottom. Conductivity and pH were measured in the laboratory as soon as possible after the samples were taken.

For limnochemical characterisation, surface and bottom water samples were taken from the centres of the lakes investigated. These were taken on four occasions: during the high water period (beginning of July), at falling water (end of September), at low water (beginning of January) and at rising water (end of April). One of the two replicate samples of each was preserved with concentrated H₂SO₄ and the other was untreated. Total P, total N, K⁺, Na⁺, Mg⁺⁺ and Ca⁺⁺ were determined. The methods used were generally those used by SCHMIDT (1972a), and K⁺ and Na⁺ were determined on the flame photometer¹⁾.

Sediment samples were taken at the fixed central lake sampling stations at falling water (September 1971) and at rising water (February 1972) and predried unfixed at 60°C before analysis for particle size and content of organically bound carbon by the COD method²⁾.

- I would like to thank Mrs. M. Mentz and Miss H. Willer, Plön, for doing the analysis in our soil laboratory.
- My thanks to Dr. U. Förstner, Institute of Mineralogy and Petrography, University of Heidelberg, for doing the particle size analysis, and to Dr. K. Furch and Mr. J. Dieterich, Plön, for doing the C_{org} determinations.

4. Lago Tupé

4.1. Abiotic factors

4.1.1. Situation and morphology

Lago Tupé is situated on the left bank of the Rio Negro, 28 km upstream from Manaus (Fig. 3). The length is 3 km, the maximum width 0.3 km and the surface area approximately 68 ha (calculated by planimetry from an aerial photograph). As the elongated form and the markedly dissected shoreline clearly show, it is a fresh water ria basin and is therefore a submerged deeply cut v-shaped valley. The edges of such a "ria lake" are correspondingly rather steep with no distinct shoreline bank. Lago Tupé has numerous inflows which are without exception of black and clear water types in the sense of SCHMIDT (1972). The

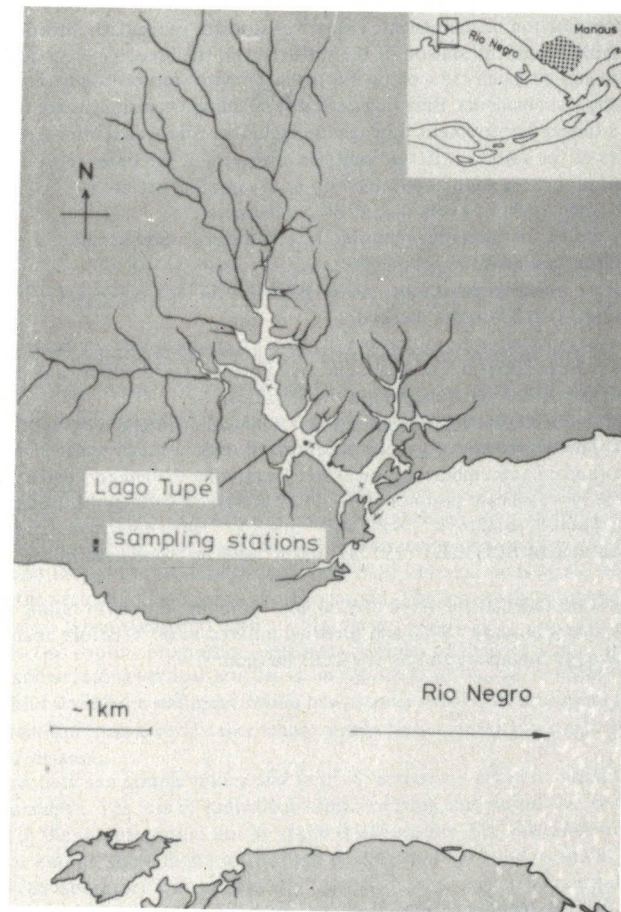


Fig. 3: Location and form of Lago Tupé, with the sampling stations (drawn from an aerial photograph, INPA, Manaus).

lake can therefore be characterised as a black water lake. The influence of white water which flows from the Rio Solimões through several cannals into the Rio Negro and thence into Lago Tupé has not as yet been considered.

The entry of Lago Tupé into the Rio Negro is displaced upstream by a sand bank extending in front of the mouth. This striking feature could be the result of a localised current in the Rio Negro. Just above Lago Tupé it consists of a stretch only 2.2 km wide formed of sandstone layers. According to FITTKAU (1974 a: 113) there was a large waterfall here during the pleistocene. It can be argued that the shoreline current flowing upstream from the 10 km wide Tarumã bay, which is on the Rio Negro downstream from Lago Tupé, is responsible for the sand bank deposition at the Lago Tupé mouth. This current is the result of the narrowing of the Rio Negro.

Maximum and minimum water depths in the lake during the sampling period were 14 m and 6 m respectively. In years of lower water level, the minimum is a few meters lower as mentioned earlier.

On the banks of the lake is a narrow strip of inundated forest or "igapó" (Fig. 4), which is extensive only in shallower areas. In species composition it seems to resemble the igapó of the nearby Rio Tarumã Mirim described by IRMLER (1974). Further up the slopes of the banks is terra firme forest which has been disturbed in only a few patches by burning of shifting cultivation. As can be expected, there are no cattle pastures near this black water lake, also no floating meadows or submerged vegetation except for very small stands of *Utricularia*.



Fig. 4: Mouth region of Lago Tupé at high water (14.8.1971).

4.1.2. Lake Sediments

The deep sediments of Lago Tupé consist of very soft, ochre-coloured mud into which the bottom sampler enters easily. The percentage particle size distribution is shown in Table 1.

Table 1: Percentage particle size distribution and content of organically bound carbon in the deep sediments of Lago Tupé.

	Clay < 2 μ	Silt 2-63 μ	Sand > 63 μ	C _{org.}
IX. 1971	27.7	46.9	28.4	9.3
II. 1972	37.1	42.8	20.1	10.2
Mean	30.9	44.9	24.3	9.8

Since it is a ria lake, Lago Tupé has a high proportion of sand in its deep sediments; this is much lower (maximum 9.5 %) in the várzea lakes investigated. In the sieved bottom fauna samples there was also a high proportion of sand amongst the particles of size greater than 400 μ . The values increase markedly from the parts of the lake nearest the Rio Negro in the direction of the terra firme (Table 2), indicating that the sands originate in the lake inflows.

Table 2: Percentage sand and detritus in the fraction of particle size greater than 400 μ in the deep sediments of Lago Tupé, along the length of the lake (sampling stations are marked X in Fig. 3).

	Mouth	Sampling station	Above sampling station
% Sand	24.9 29.4	62.2	81.5
% Detritus	75.6 70.6	37.8	18.5

The detritus in the sieve remains is almost always coarse i.e. it contains complete leaves, pieces of branches, almost unbroken twigs and various plant seeds and fruits which are normally black in colour. Isolated parts of the chitinous cuticles of terrestrial insects are also found. The steep banks and narrow basin of Lago Tupé allow the entry of almost unbroken allochthonous material into the deep sediments, where it can be preserved intact for long periods under the still unknown chemical conditions.

The content of organically bound carbon (Table 1) of the deep sediments is very high (mean 10 %) in contrast to that of the várzea lakes (maximum 5.5 %). This is probably due to the presence of sedimented humic compounds.

The sediments of the shore region originate either from firm inundated igapó soils with a litter layer which varies with the time of year, or from the similarly firm, higher, vegetation-free sandy-clay shore slopes gradually merge into the soft deep mud. Between the lake margin of the igapó and the shore slope is a relatively narrow zone which is periodically covered with a thin layer of algae. Apart from diatoms, this layer consists mainly of the filamentous blue green alga *Hapalosiphon* sp., a genus of which several thermophilic

species also occur in Europe, as well as isolated *Lyngbya* sp. and other small unnamed blue green algae¹⁾. The importance of this layer of diatoms and blue green algae as substrate and food source for the littoral fauna is discussed later.

4.1.3. Water level fluctuations and Secchi transparency

The water level of Lago Tupé is determined mainly by that of the Rio Negro and somewhat less by the inflows to the lake. The water level curves of lake (Fig. 5) and river (Fig. 2) are similar; any deviations are because the lake level was only measured at monthly intervals while that of the river was measured daily. The water level was lowest (6 m) in November and highest (14 m) in June and July.

The Secchi transparency in the Rio Negro (measured in the middle of the river at the level of Lago Tupé) varies only between 1.4 and 2.0 during the year; values for Lago Tupé, however, vary slightly more (between 1.4 and 2.7 m) as shown in Fig. 5. The maximum value of 2.7 m coincides with the high rainfall in November; presumably the large amounts of rain water running in to the lake at this time have a dilution effect and the Secchi trans-

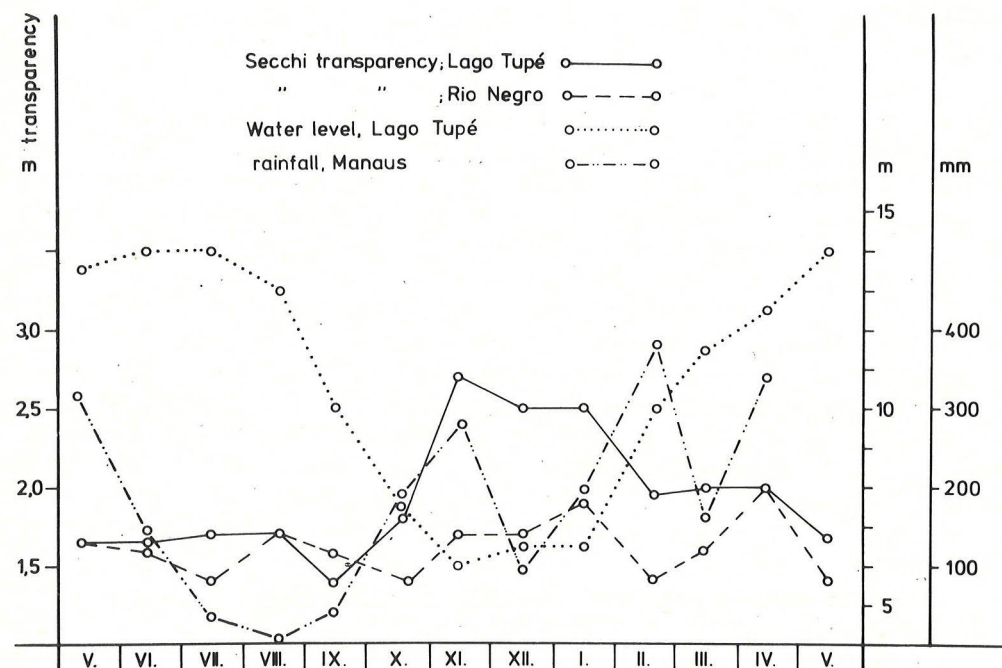


Fig. 5: Annual pattern of Secchi transparency in Lago Tupé and the Rio Negro together with the water levels in the lake and the monthly means of precipitation at the weather station at Manaus.

1) I wish to express my thanks to Dr. H. Schwabe, Plön, for the identifications.

parency therefore increases. In February, however, when high rainfall combined with rising water level i.e. entry of relatively low transparency Rio Negro water in to the lake, the Secchi transparency decreases slowly to levels found in the Rio Negro. Particularly at high water, therefore, the lake can contain, at least on the surface, water which has entered from the Rio Negro.

4.1.4. Temperature and oxygen concentrations

Lago Tupé showed a clear temperature and oxygen stratification throughout the sampling period (Fig. 6). In the lake middle, surface temperatures ranged from 28.0 to 34.0°C, and the bottom was considerably cooler, from 25.3 to 27.0°C. The relatively low (in comparison with the várzea lakes) temperatures of the deeper water layers presumably means that the water of the terra firme streams, which is at about 24°C, feeding the lake forms a layer at the bottom. The surface temperature was highest in September, the driest month, and conditions therefore were most favourable for stratification then, while at the end of the low water phase (January) the temperature difference between surface and profundal water layers was lowest. Oxygen concentrations of the profundal waters were highest at this time, reaching values of 0.6 mg/l (7.8 % saturation); for the rest of the sampling period the values were 0.1 to 0.3 mg/l (1.0 to 3.8 % saturation). As would be expected, surface oxygen concentrations were high, reaching values of 5.1 (67.2 % saturation) to 6.4 (84.6 % saturation) mg/l.

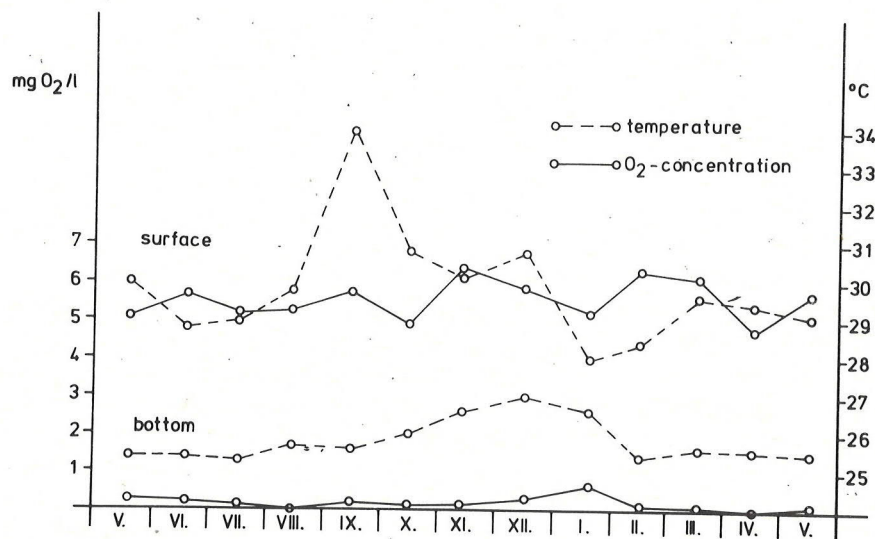


Fig. 6: Annual pattern of temperature and oxygen concentrations of the surface and bottom water in Lago Tupé.

A vertical profile taken in the lake middle during the high water phase (Fig. 7) showed the presence of an upper thermocline at 2-3 m and a lower one at 7-10 m. The hypolimnion was homothermic.

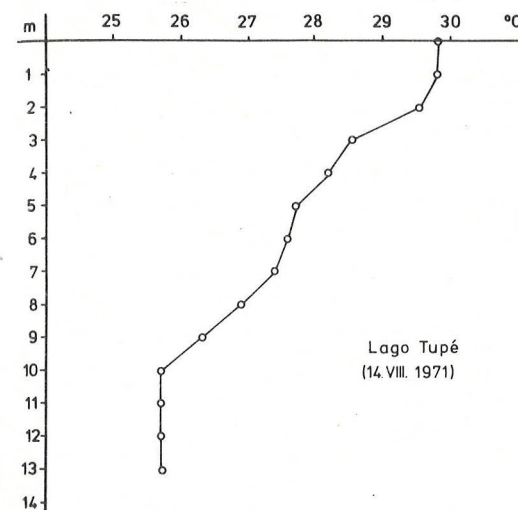


Fig. 7: Vertical profile of temperature in the lake middle during the high water period.

As shown by SCHMIDT (1973 a) for the várzea lake, Lago do Castanho, full turnover at water levels greater than 5 m can seldom be expected, but at low water levels, partial and full turnover could be demonstrated. This is also true for Lago Tupé which, at low water, turns over even less frequently than Lago do Castanho. This latter lake is similarly protected from the wind. This is because its length is transverse to the prevailing wind direction and also, since it is narrow and the banks steep, strong winds have little effect. Thus Lago Tupé can presumably stagnate even at water depths less than 5 m.

From these stratification characteristics, Lago Tupé can be designated an oligo- to polymictic lake, which underwent a phase of "thermal meromixis" (LÖFFLER 1957:40) during the sampling period. The accompanying poor oxygen supply in the hypolimnion certainly had an adverse effect on the quantitative development of the benthic fauna compared with years of one or more complete turnovers during the low water period. The qualitative composition of the fauna, however, should not exhibit much change as a result of a temporary oxygen deficiency in the profundal water layers.

From mid-June (maximum water level) to mid-November (minimum water level) a slight to moderately strong smell of H₂S was evident but none could be detected later in the low water phase or during the period of rising water level. The probable effect of H₂S in the bottom water layers on the total abundance of the zoobenthos is discussed later.

4.1.5. Conductivity and pH

The characteristic electrolyte poorness and low pH values of Amazon black waters has been discussed by SIOLI (1951 b, 1955, 1956). In this context, however, reference is especially made to the intensive limnochemical investigation of H. UNGEMACH in the Rio Negro just above Manaus (Anonymus 1972), since these data fit in with his picture. Both conductivity and pH remain almost constant with no distinct maxima or minima (Figs. 8 and 9). In the Rio Negro the pH varies between 4.4 and 5.5 and in Lago Tupé

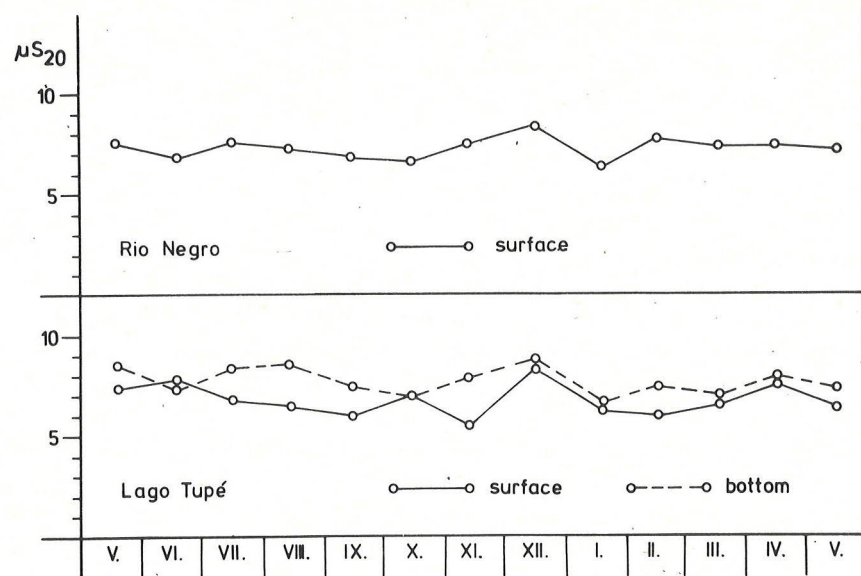


Fig. 8: Annual pattern of conductivity in the Rio Negro and Lago Tupé.

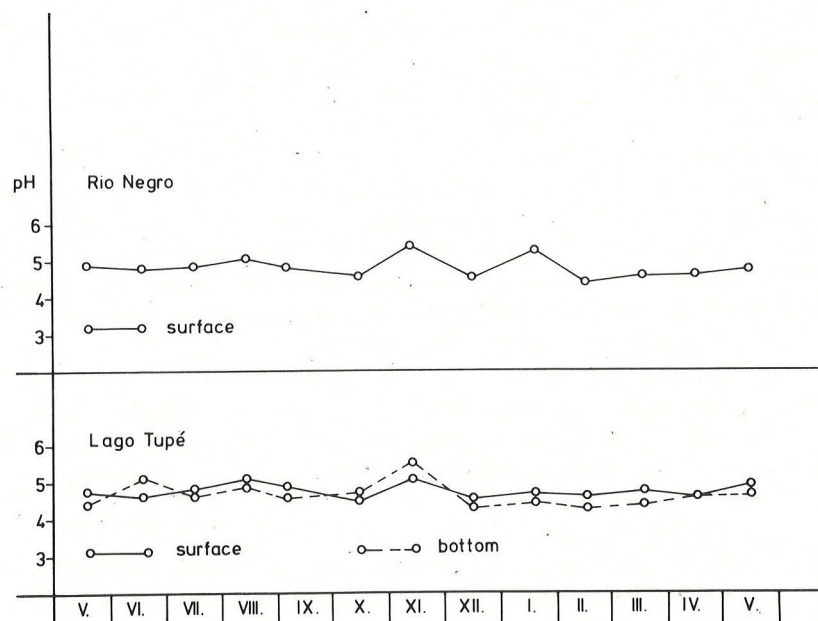


Fig. 9: Annual pattern of pH in the Rio Negro and Lago Tupé.

between 4.5 and 5.1 at the surface and 4.3 - 5.5 near the bottom. The conductivity of the Rio Negro is 6.3 - 8.4 μS_{20} (mean 7.31) and in Lago Tupé 5.7 - 8.4 μS_{20} (mean 6.82) at the surface and 6.6 - 8.8 μS_{20} (mean 7.8) at the bottom. The bottom water layers contain more electrolytes than those at the surface as a result of the chemical exchange processes between the sediments and the water body. It seems that pH and conductivity do not depend on the water level.

4.1.6. Other limnochemical factors

Lago Tupé was characterised limnochemically by analysing four sets of water samples, taken at maximum and minimum water levels, and in the period of falling and rising water level (Table 3). Only the analysis from the fixed water samples were used.

Table 3: Comparison of the concentrations of some elements in the waters of Lago Tupé (surface and 0,5 m above the bottom), Rio Negro, and five terra firme streams.

γ/l		Lago Tupé (fixed samples)					Rio Negro O m (ANONYMUS, 1972)		Terra firme streams (SCHMIDT, 1972 b)	
		16.VII.71 (13,5 m)	71 15.X. (7m)	18.I.72 (6m)	17.IV. 72 (12m)		monthly mean			
							V	M	V	M
Na ⁺	O m	380	280	240	350	271	435-1358	719	190-210	200
	Bottom	330	230	180	180		-	-	-	-
K ⁺	O m	100	140	<50	100	<84	235- 601	435	80-170	125
	Bottom	70	110	<50	<50		-	-	-	-
Mg ⁺⁺	O m	130	130	100	-	110	108- 254	172	<10- 16	<10
	Bottom	100	100	100	-		-	-	-	-
Ca ⁺⁺	O m	1040	1040	560	360	605	232- 450	336	<20	<20
	Bottom	560	640	440	200		-	-	-	-
P _{total}	O m	23	12	16	12	15,6	4,8- 14	8,8	2-5	3,4
	Bottom	20	16	13	13		-	-	-	-
N _{total}	O m	530	520	130	495	397	302- 575	394	130-190	170
	Bottom	410	350	195	545		-	-	-	-

Contrary to expectations, the figures show no obvious annual pattern. The finding (Anonymus 1972) for the lower Rio Negro that the ionic concentrations increase and decrease with the water level is apparently not true for Lago Tupé. When one compares the values from the lake with those of the Rio Negro and terra firme streams, it is seen that the element concentrations in the lake waters fall within the range of variation of these running waters (Table 3). An exception is the total P content which is higher in both surface and bottom water than in the inflows. Since all values, however, are at the lower limits of detectability and are therefore susceptible to errors in the method, more extensive investigations are needed to establish the presence of a possible internal phosphate budget in black water lakes. Better methods are similarly needed for determining concentrations of potassium which in some cases are considerably lower in the lake than in the inflowing waters.

Another striking feature of Lago Tupé is that the elements measured are present in smaller quantities in the bottom than in the surface water. This could be a result of strati-

fication of the relatively cool, electrolyte-poor stream water in the lake depths. This is particularly marked with the alkali and alkaline earth metals.

4.2. The macrozoobenthos

As mentioned earlier, the benthic fauna was investigated at two locally fixed sampling stations (Fig. 3). The station in the lake middle, from which 48 samples were taken, was about 100 m from the shore and 1 km from the lake outflow. The fauna at the shore sampling station could not be sampled over a full year (see chapter 3) and the 19 samples taken there only extend over 7 months, from November 1971 to May 1972.

4.2.1. The profundal fauna

Both densities of individuals and biomass values in the sediments were low because of the persistent thermal stratification of the lake and the related poor oxygen supply in the hypolimnion. The mean total abundance for the year was low, at 721 individuals/m² with a minimum of 66 individuals/m² in August when the water level decreased rapidly, and a maximum of 1705 individuals/m² in April when the water level was rapidly rising (Fig. 10). There is no apparent correlation between oxygen content of the bottom water layers (Fig. 6) and total abundance.

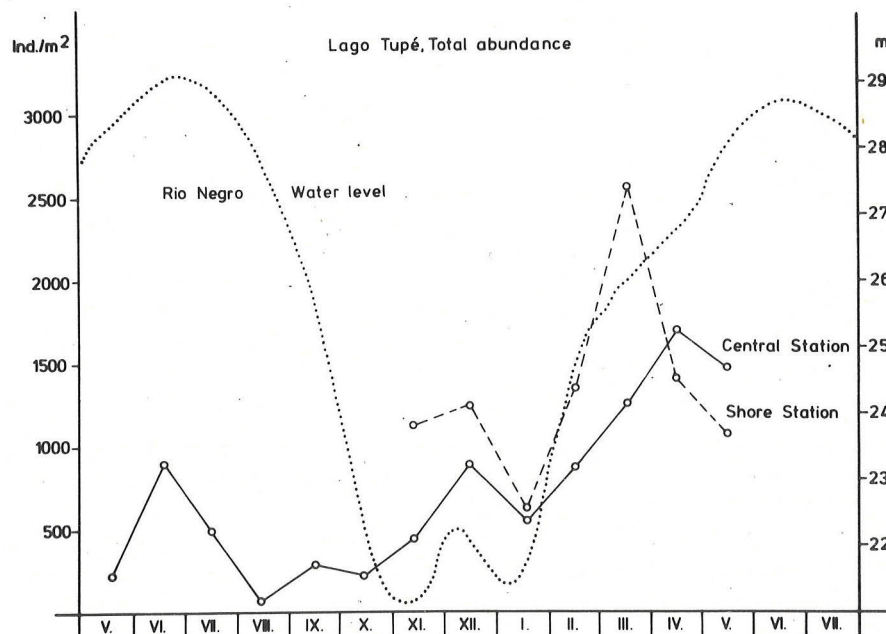


Fig. 10: Annual pattern of total abundance of the zoobenthos in Lago Tupé at the lake central and shore stations (beginning at minimum water level).

There is possibly a relationship between abundance of zoobenthos and H₂S concentration in the bottom water layers. The gas can be detected in variable intensity by smell during the entire falling water phase, beginning with maximum water level and ending with minimum water level; highest values are between August and October and these coincide with the lowest figures for abundance. In June, July and November the H₂S smell is weak and the abundance values higher than in the intervening months. From December and during the whole period of rising water there is no smell of H₂S and the abundance values reach their maximum levels. It therefore seems that total abundance is very much influenced by the H₂S concentration.

In view of the unfavourable environmental conditions it is not surprising that the profundal fauna consists of only four groups of animals - Chaoboridae, Ostracoda, Acari and Nematoda. The latter need not even be considered since they only occur in November and December in low numbers (15 individuals/m² i.e. 0.3 % of the mean annual total abundance of the profundal fauna). The few individuals found belong to the sub-order Dorylaimina and to the family Mermithidae.

Abundance values for the other three groups over the year are shown in Fig. 11; with Chaoboridae and Ostracoda the figures show a clear pattern. For Chaoboridae the highest density, with a maximum of 445 individuals/m² was attained during the low water phase and when the water level was rising rapidly i.e. from November to April. Few or no chaoborid larvae were found in the profundal sediments at maximum water level and at rapidly falling water level. The mean annual abundance is 192 individuals/m², i.e. 27 % of the mean annual total abundance.

The Ostracoda were far more frequent with a mean annual total abundance of 457 individuals/m², i.e. 63 % of the mean annual total. The maximum density of 1275 individuals/m² was at rapidly rising water level and at maximum water level i.e. between March and June. As with the Chaoboridae, the abundance decreased markedly at falling water.

Figures for the Acari show no clear annual pattern. The maximum of 148 individuals/m² is in the low water phase and the mean annual abundance is 70 individuals/m², i.e. 10 % of the mean annual total.

From the above it is clear that total abundance reaches a maximum at rapidly rising water (Fig. 11) because the abundance of ostracods is maximum at this time.

The profundal zoocoenoses of Lago Tupé can be further characterised by examining the figures for group dominance over the year (Fig. 12). At high water levels, i.e. from February to September, regardless of whether the water level is rising or falling, the Ostracoda are dominant (38-88 % of total fauna). At the low water between October and January, chaoborid larvae are dominant (35-83 %). Thus Chaoboridae have the highest dominance values at minimum water levels while for the Ostracoda this happens at or just before the time of maximum water level.

The Acari play a minor role in both dominance and abundance. Only in September and October are their dominance values the same as those of the Ostracoda (38 %) and the Chaoboridae (35 %) respectively.

Although the mean annual abundance of 721 individuals/m² found in Lago Tupé is not very low compared with the white water várzea lakes (Lago Muratú 736 individuals/m², Lago dos Passarinhos 810 individuals/m²), the mean total biomass of the central region of

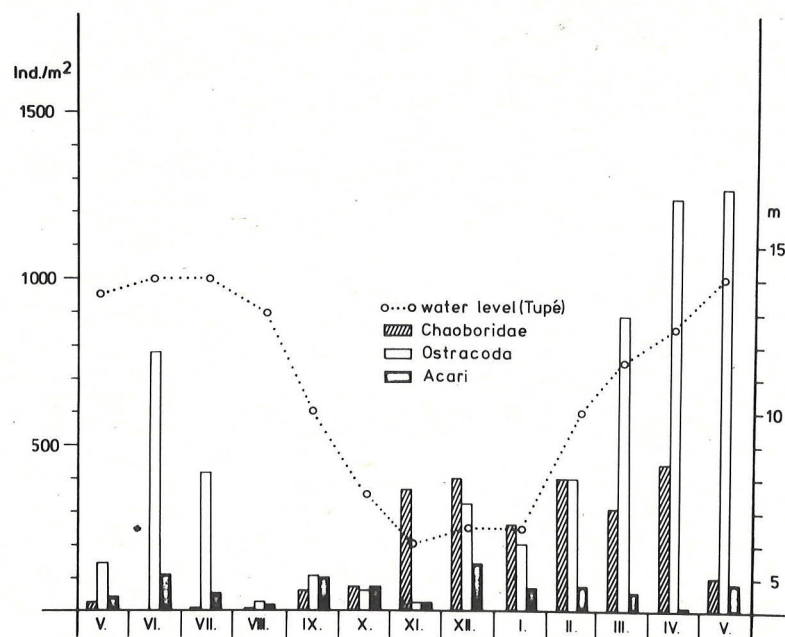


Fig. 11: Annual pattern of abundance of the animal groups (excluding Nematoda) found in the profundal zone of Lago Tupé.

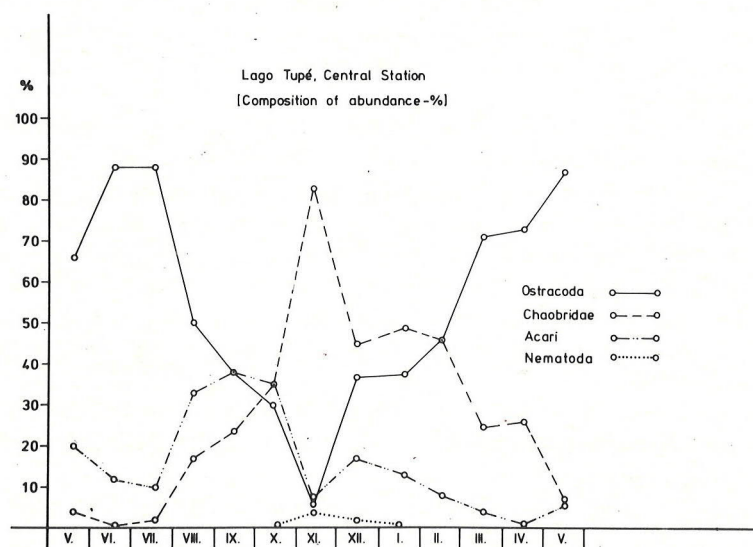


Fig. 12: Annual pattern of group dominance in the profundal zoocenose of Lago Tupé.

Lago Tupé is much lower, being $0,136 \text{ g/m}^2$ wet weight, while it is $2,65$ and $2,06 \text{ g/m}^2$ in Lago Muratú and Lago dos Passarinhos respectively. This is because the groups of animals constituting the profundal fauna of Lago Tupé (Ostracoda, Chaoboridae, Acari) include only small, light individuals, while in the sediments of the white water lakes there are large heavy chironomid and ephemeropteran larvae. Lago Tupé has the lowest mean annual total biomass of all the lakes investigated in the Central Amazon.

Fig. 13 shows that the biomass exhibits little annual variation. The maximum values of $0,23$ - $0,24 \text{ g/m}^2$, corresponding also to maximum abundance, are found when the water level is low or rising, and the minima occur in August when the water level is falling.

The seasonal distribution of biomass dominance is shown in Fig. 14. The Ostracoda are dominant with a relative biomass making up 40 - 73 % of the total at high water between May and July. At low and rising water the Chaoboridae dominate with a relative biomass of 53 - 92 %, giving way to the Acari (62 - 100 %) at falling water in August and September. The mean annual total biomass is $0,136 \text{ g/m}^2$, comprising 54 % Chaoboridae, 29 % Ostracoda and 17 % Acari. The Nematoda (less than 1 %) are not shown in Fig. 14.

The profundal zoocenose of Lago Tupé can be characterised as follows:

- (1) It has the lowest mean abundance of all the lakes investigated (721 individuals/ m^2 over the year) with a maximum of only 2360 individuals/ m^2 in June 1971.
- (2) Group diversity is low with certain individual groups being well-represented throughout the year. The Nematoda are seldom found but the other three groups were present every month except June when the Chaoboridae were absent.
- (3) The mean biomass value ($0,136 \text{ g/m}^2$ over the year) is the lowest of all the lakes investigated. The value for Lago Jacaretinga, a lake in the Central Amazon várzea, is $45,5$ times higher.
- (4) Total abundance and to a lesser degree, total biomass show an annual periodicity which is at least partly due to the water level fluctuations.

At present not much is known about species number, as identification of all the animals sampled is not yet complete. However, it is reasonable to assume that with low group number and unfavourable environmental conditions in the depths of the lake, each group has only one dominant species. Minor species occur for short periods depending on the conditions prevailing. There is some evidence for this assumption in that provisional determinations of the Acari show that 82 % of the individuals belong to the species *Krendowskia* (*Krendowskiella*) sp. The Chaoboridae also provide some evidence. Pupal skins drifting on the lake surface were collected in November, February and April, and two species were distinguished in the ratio $10:1$. Pupae of the common one were also found in the profundal and shore sediments and presumably most of the larvae found belong to this species. It is uncertain whether the larvae of the less common species also colonise the lake sediments or whether the pupal skins merely drifted in from other biotopes e.g. the igapó.

It appears also that there are few species of Ostracoda.

Since it seems likely that there is a limited number of species in the profundal zoocenose of Lago Tupé, it is also likely that the feeding interactions are simple. The main food source are the numerous detritophagous Ostracoda, and the Acari, belonging mainly to the family Krendowskiidae LUNDBLAD 1930, are their principal consumers. Hitherto there have been no direct feeding observations but the mouth parts are morphologically very similar to those of the related family, the Arrenuridae (D. Stechmann, in litt.) which

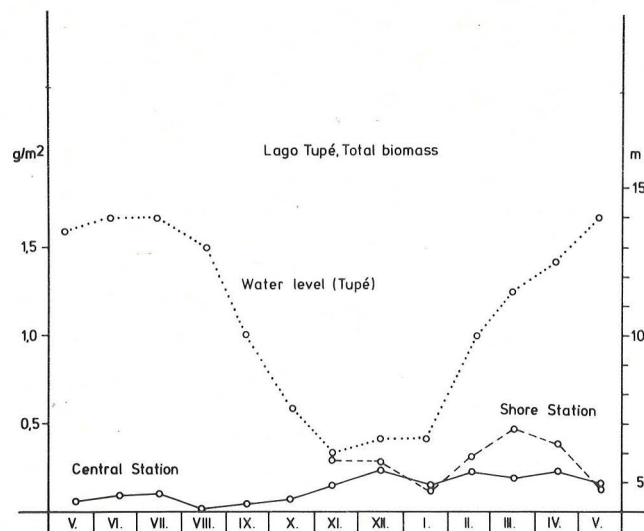


Fig. 13: Annual pattern of total biomass of the zoobenthos in Lago Tupé in the lake middle and at the shore (beginning at minimum water level).

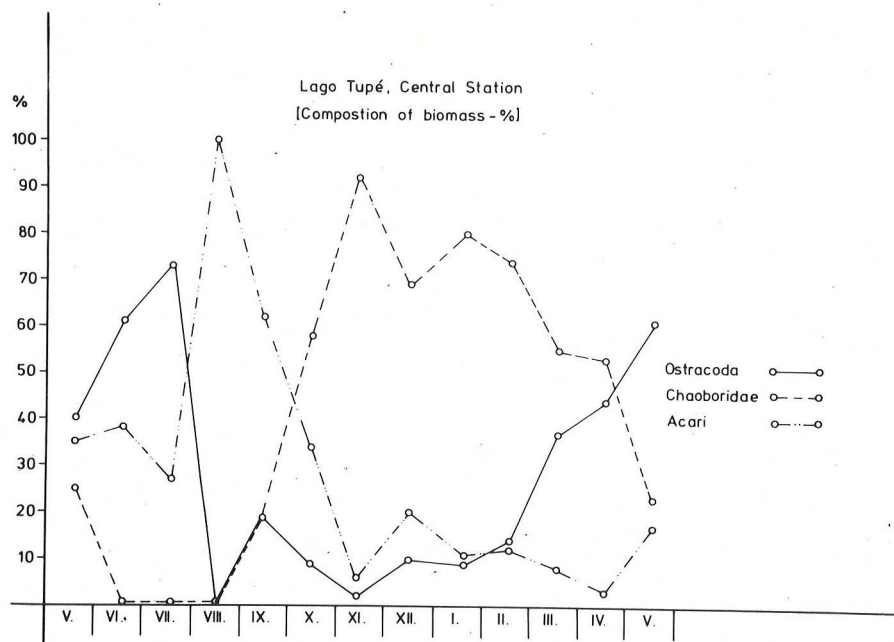


Fig. 14: Annual pattern of biomass dominance in the profundal zoocoenose of Lago Tupé.

feeds avidly on Ostracoda, Copepoda and Cladocera (BÖTTGER 1970). One can assume that the above mentioned *Krendowskia* sp. feed on the only small crabs found here, the Ostracoda.

The larvae of the Chaoboridae are also carnivorous; according to PARMA (1971) the European *Chaoborus* sp. feeds mainly on zooplankton with Copepoda being favoured over Cladocera and Rotatoria, and they also feed on benthic organisms such as larvae of Harpacticidae, Ephemeroptera and Chironomidae. It is likely that the chaoborid larvae of the Central Amazon lakes have a similar food spectrum and Ostracoda would therefore form a certain part of their food, but there have been no direct observations. The chaoborid larvae in their daily vertical migrations feed preferably on allochthonous zooplankton of the epilimnion, and they could thus be important in the nutrient supply of the profundal benthic fauna by providing a supply of excrement and food remains for the profundal zoocoenose. In a stratified tropical water body the zoo- and phytoplankton of the epilimnion are broken down by bacteria in the thermocline and cannot form a food source for the benthic zoocoenose.

4.2.2. The littoral fauna

Starting at minimum water level in November the total abundance and biomass of the littoral zoobenthos were also measured at monthly intervals. The seasonal pattern of total abundance (Fig. 10) resembles that of the profundal fauna. The maximum value (2559 individuals/m²), found when the water was rising rapidly, is much higher, and it decreases sharply at maximum water level, falling to a minimum at decreasing water level. There is a smaller abundance peak in the low water phase (1248 individuals/m² in December) followed by a minimum (623 individuals/m² in January). This curve can be interpreted by looking at group abundances in Fig. 15. It appears that the faunal group composition differs at periods of minimum (November to January) and increasing (February to May) water level; there is an almost complete change in composition between mid-January and mid-February. At low water (depth 0,4 to 0,7 m) the Chironomidae dominate (43-74 % of the total fauna); Oligochaeta, Acari, Caenidae and Corixidae as well as other minor groups are also present. Over the next month the water level rises by about 3,5 m and in mid-February is around 4 m resulting in replacement of the above groups with Chaoboridae and Ostracoda. As the water level rises further the abundance of particularly the Chaoboridae increases, reaching a maximum of 2180 individuals/m² in March, decreasing sharply towards the period of maximum water level. The Ostracoda are present in lesser numbers and reached the maximum of 415 individuals/m² in May when the water level was 8 m.

Thus at the fixed littoral sampling station the littoral fauna consists of a large number of groups around the low water period; at rising water the fauna has fewer groups and in composition resembles the profundal fauna. If the completed identifications of the Chaoboridae and Ostracoda show that the same species are present in both profundal and littoral zones at rising water level, migration becomes a distinct possibility. It is most unlikely that an individual density figure of 1008 individuals/m² could develop from eggs within a month by chance from a locality with initially no chaoborid larvae (see Fig. 15). It is not yet clear whether the littoral populations of Chaoboridae arise from vertical migrations of profundal fauna or from the planktonic-living section of the population.

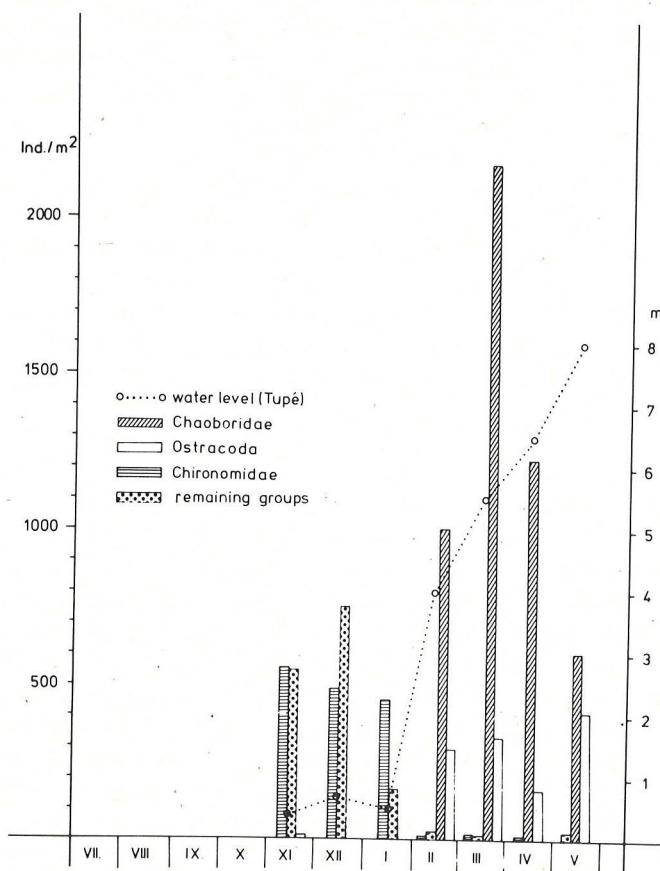


Fig. 15: Abundance of the dominant animal groups of the littoral zone of Lago Tupé from November 1971 to May 1972, together with the water level curve of the shore sampling station.

The rapid qualitative and quantitative changes in the composition of the littoral fauna when the water level begins to rise are probably due to rapidly declining oxygen concentrations in the bottom water layers. One available determination showed the oxygen concentration to be only 0,7 mg/l recorded on 18.3.1972 at a depth of 5 m (0,5 m above the bottom).

The true littoral fauna occurs in the peripheral zone of the lake in water depths of 0 to 1,5 m and at a maximum depth of 2 m. With rising and falling water level the zone is displaced towards the igapó and the lake respectively. The zone can increase in width at decreasing water level provided that the water is not at the critical depth of 5 m with accompanying turnover and oxygen deficit.

The littoral fauna is affected by the nature of the substrate as well as by water depth and oxygen supply. The substrate of the littoral region consists of compact clayey sands of

the tertiary Alter do Chão formation with a very sparse plant cover. There is a semi-igapó vegetation type consisting of diffuse short trees and bushes, merging into a treeless zone especially in the steeper areas. This zone is covered in places with a sparse grass growth and when flooded is covered by a thin layer of the blue green alga *Hapalosiphon* sp. and diatoms. Stomach content analyses show that these are an important food source for the phytophagous littoral benthic species, especially, the larvae of the Chironominae. Diatoms and *Hapalosiphon* sp. cannot occur further lakewards because of the substrate change from compact littoral sediment to the soft mud of the lake basin; likewise they do not appear to occur on the igapó soils (IRMLER 1974). Their development is probably prevented by the dense litter covering the soil, which is covered with a gel-like layer of humus, and by the low light intensity. The film of *Hapalosiphon* seems to be little influenced by inundation since it was found in water 6,5 m deep at the littoral sampling station on 17.4.1972.

The characteristic littoral fauna can therefore only develop in a "potential" lake littoral zone, designated in this paper as the genuine littoral zone (Fig. 16). On either side of this zone the substrate is the limiting factor. The exact position and extent of the zone are determined within these boundaries by the water level. If the shoreline is displaced at rising water level into the igapó, the characteristic zoocenose for this biotope develops, as described by IRMLER (1974). The genuine littoral zone is then occupied by a zoocenose which is qualitatively almost identical with that of the profundal zone. When the water level drops, the igapó normally dries out completely and a littoral zoocenose can again develop at the lake edge. The existence of this is jeopardised only if the water level becomes lower than the average minimum (less than 1 m in Lago Tupé), which seldom happens.

As well as tolerating these conditions, the littoral fauna must also survive the annual high water phase during which the true littoral zone is unavailable to them. The same applies to the aquatic igapó fauna during low water.

An insight into how all, or part, of the littoral fauna survives the high water period was obtained by dividing the fauna as far as possible into groups with similar abundance values so that comparisons with the igapó fauna are possible. The igapó substrate is suitable and the water shallow and well-oxygenated so that the littoral fauna can easily survive here. In fact the igapó can be considered as a special part of the littoral zone since the two habitats have more in common with each other than with the profundal zone of the lake.

In Tables 4 and 5 all the taxa so far known from the littoral zone are shown, together with their abundance values. With the exception of the chironomid genus *Tanytarsus* all the taxa show maximum abundance at the beginning or middle of the low water phase and decrease sharply at the end of this phase in January when some taxa are no longer identifiable. Since there are many different taxa involved, this decrease cannot really be explained as being a transition into the egg phase or a resting stage, in which the high water phase could be survived.

Simultaneous investigations of the benthic faunal composition of the Rio Tarumã-Mirim a few km from Lago Tupé showed that there are many species common to the two biotopes: *Opisthocysta flagellum*, *Brasilocaenis irmleri*, *Chironomus paragigas*, *Chironomus* sp. AR 4 and *Tanytarsus* sp. 2, with other common species expected among the Naididae, Tanypodinae and the genera *Polypedilum* and *Tanytarsus*. Thus one-third or more of the species found are common to lake littoral and igapó. This leads to the speculation that there is migration of species between the biotopes. This is supported by Irmler (l.c.) who

	Oligochaeta (Opisthocysta flagellum, Tubificidae, Naididae)	Hirudinea	Cladocera	Acanthi	Trichoptera	Brasiliocaelis irmleri (Cae- nidae)	Odonata	Tenagobia selecta (Co- ridae)	Ceratopogonidae
13.XI.	-	-	15	45	29	29	-	414	15
16.XII.	267	-	89	178	-	134	45	45	-
18.I.	134	-	15	-	-	15	-	-	-
17.II.	29	-	-	-	-	-	-	-	-
18.III.	-	22	-	-	-	-	-	-	-
17.IV.	-	-	-	-	-	-	-	-	-
16.V.	29	-	-	-	-	-	-	-	-

Table 4: Abundances (individuals/m²) of the genuine subdominant animal groups of the littoral zone of Lago Tupé (remaining groups of fig. 15).

	Tanypodi- nae (5 spe- cies)	Orthocla- diinae (1 species)	Chirono- mus sp. AR 4	Chiro- nomus paragigas	Zavreliella sp.	Chironomi- ni gen. A 2 sp. A 2	Polypedi- lum (seve- ral species)	Chirono- mini lar- vae type 1	Chironomi lar- vae type 3	Tanytar- sus (2 spe- cies)
13.XI.	225	15	90	-	-	30	60	15	-	135
16.XII.	180	-	-	135	45	45	-	45	45	180
18.I.	30	-	15	15	-	15	45	15	15	239
17.II.	-	-	-	-	15	-	-	-	-	-
18.III.	-	-	-	30	-	-	-	-	-	-
17.IV.	-	-	-	-	-	-	15	-	-	-
16.V.	-	-	-	-	-	-	-	-	-	-

Table 5: Abundances of chironomid larvae (individuals/m²) of the littoral zone of Lago Tupé.

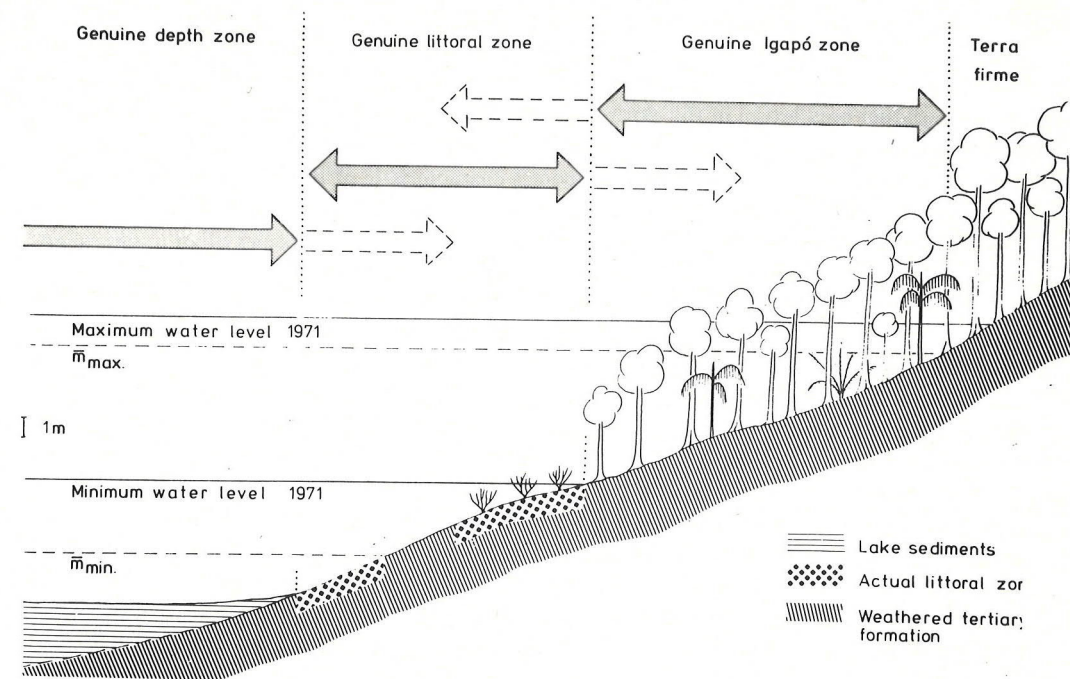


Fig. 16: Scheme for vertical zonation of the aquatic benthic fauna in an Amazon black water lake and the neighbouring igapó. The borders of the three zones (dotted lines) are determined by the type of substrate and vegetation. Within the framework of the given factors, true profundal, littoral and igapó zoocoenoses can develop (black arrows). The actual location and extent of the zoocoenoses are determined by the water level at the time (symbolised here by maximum and minimum water level 1971, as well as by the mean maximum and minimum water level) and the corresponding oxygen concentration of the bottom water layers (see text). Part of the zoocoenose (broken arrow) shows, as adaptation to the annual rhythmic level fluctuations, the ability to migrate into neighbouring zones. Such faunal movements are not only a feature of Amazon black water biotopes; they occur also in modified form in mixed and white water biotopes.

found that there was a movement of species in the igapó itself especially at rising water, with the shrimp *Euryrhynchus burchelli*, the Naididae and also *Polypedium* and *Brasiliacaelis irmleri*. Such migration are possibly the commonest method of adapting to the large water-level fluctuations by the fauna concerned. This therefore makes it difficult in many cases to say whether such a migratory species, which can colonise the two biotopes in comparable numbers, prefers the littoral or the igapó zone, i.e. whether it is a genuine littoral or igapó species. The high abundance values in the igapó of a group such as the Naididae (Irmeler l.c.) suggest that it is a genuine igapó species which survives the low water phase only as a residual population in the lake littoral zone.

The lake littoral zone provides refuge for the inhabitants of other biotopes during the low water period. REISS (1974) showed this for the larvae of a prolific chironomid coloniser of the floating meadows of várzea lakes, *Goeldichironomus natans*; there is a permanent residual population in the littoral sediments from which the floating meadows, which dry up and die at low water, can once more be colonised when they re-form at rising water.

There are also genuine littoral zone species characteristic of this zoocenose as is shown by the presence of some chironomid species reared from littoral sediments, of which hitherto only adults and pupae but not larvae were known. These are the species of an undescribed genus of the Chironomini, genus A 13 species A 4, and *Tanytarsus* sp. 10, another species of this group. It may correspond to the Chironomini larval type 3 which appears in Table 5. The *Tanytarsus* larvae mentioned there possibly belong to *Tanytarsus* sp. 2 and sp. 10 which belong to the same species group, and the larvae may be difficult to distinguish. *Tanytarsus* sp. 10 and Chironomini genus A 13 sp. A 4 were also found in the littoral sediments of the várzea lakes but not among the benthos of the igapó or other lacustrine biotopes of the Central Amazon.

In the littoral benthic fauna of Lago Tupé there are also species which are usually found in greatest numbers in the floating vegetation of the várzea lakes, such as *Tenagobia selecta* (see JUNK 1973), another undescribed chironomid genus, Chironomini genus A 2 sp. A 2 and *Zavreliella* sp., a chironomid whose larvae live in trichopteran-like cases. The occurrence of these species in a black water lake devoid of floating vegetation is surprising; their life cycles are possibly similar to that of *Goeldichironomus natans*. The populations of the littoral sediments form potential reservoirs for the colonisation of floating vegetation, but the above mentioned species are more tolerant than *Goeldichironomus natans* whose larvae avoid black water biotopes. The marked population changes which are characteristic of the Central Amazon aquatic ecosystems and which enable organisms to adapt to the extreme annual water level fluctuations are particularly well expressed by these species. Many plant and animal species adapt to a hydrodynamic situation in this way. Depending on the water level, they periodically leave the unfavourable biotope for a temporary new biotope whereby they try to reach a maximum of independence of water level fluctuations.

When one considers the above situations, it appears to me that it is no really meaningful to speak of a "littoral" or "igapó" species, particularly when the species can be found in both biotopes and shows no distinct preference for either.

Having examined the question of the occurrence of the same species in different biotopes with different food sources, one should naturally next consider the feeding habits of the species. According to IRMLER (1974), *Brasilocaenis irmleri* feeds in the igapó mainly phytophagously on fungal spores and hyphae and to a far lesser extent on the remains of higher plants and detritus. From investigations of stomach contents it appears that the population in the littoral zone of Lago Tupé prefers diatoms and the blue green alga *Hapalosiphon* sp. (mentioned previously), as well as fungal spores and hyphae. Higher plant remains and detritus are far less important. This indicates that feeding depends on what is immediately available, and there is no obvious specialisation. The same is true for the chironomid genera studied (*Chironomus*, *Polypedilum* and *Tanytarsus*) which feed on approximately equal quantities of diatoms, fungi and blue green algae, while in the igapó mainly plant remains and fungi are consumed. It would seem that the ability to move from one habitat to another goes hand in hand with an absence of distinct food preferences.

Another phytophagous animal is *Tenagobia selecta*. According to WESENBERG-LUND (1942) the Corixidae feed mainly on plants, and from the available evidence, especially on filamentous green algae. In Lago Tupé, *Hapalosiphon* could be the food source.

Phytophagous and detritophagous methods of feeding are found in the Oligochaeta whose gut content consisted of detritus, diatoms, fungal hyphae and fungal spores. This was very similar in composition to that of the phytophagous insect larvae mentioned above.

The zoophagous content of the littoral benthic zoocenose is dominated by the relatively numerous Tanypodinae species. These feed mainly on larvae of Chironominae and on Oligochaeta. The Tanypodinae accounted for 14,5 % of the total faunal abundance during the low water months (November to January), while the remaining zoophagous groups, the Acari, Hirudinea, Trichoptera, Odonata and Ceratopogonidae together only accounted for 10,4 %. Unfortunately there are still considerable taxonomic diagnostic difficulties with the Amazonian Tanypodinae which for the moment prevent further classification into genera and species.

When one compares the phytophagous benthic fauna of the igapó and lake littoral, there is a conspicuous preponderance of diatoms and blue green algae in the food of the littoral benthos, while in the igapó fauna, fungi predominate. This could be the result of a poorer fungal supply in the littoral zone. However, it seems more likely to me that the light deficiency in the igapó limits the growth of diatoms and blue green algae there, and consequently phytophagous species are forced to feed largely on fungi. According to IRMLER (1974 and personal communication) algae were never found in the food of benthic species in the igapó.

In addition to abundance values, total biomass was also determined monthly at the littoral sampling station (Fig. 13). Almost all values are to some extent considerably higher in the littoral than the corresponding values from the central part of the lake. A maximum of 0,64 g/m² was reached in March during maximum abundance of the Chaoboridae, while minima in January (0,144 g/m²) and May (0,139 g/m²) occur. The low biomass in January is correlated with the minimum value of total abundance (Fig. 10) during the change from the true littoral fauna of the low water period to the fauna of high water. The minimum biomass value in May shows that biomass in the littoral area, just as in the depths of the lake, decreases constantly with falling water to its lowest at this time.

The mean total biomass estimated from the seven month sampling period is 0,31 g/m² for the shore station. However it can be assumed that an annual mean value would be lower than this because between June and October, when no samples were taken, very low biomass would be expected. In the seven month mean of 0,31 g/m², the Chaoboridae predominate, accounting for 54 %, whilst the Chironomidae account for 25 % and the other groups each for 5 % or less.

5. Comparison with other Central Amazon black water lakes

The other black water lakes were only investigated with one or a few random samples per year. It should be noted again that the term black water lakes are used here refers only to those water bodies which show no detectable influence of white water. Should there be such an influence, regardless of duration or intensity, then it is a mixed water lake such as occur mostly in the várzea.

5.1. Lago do Cuieiras

"Lago do Cuieiras" is an officially unnamed small lake in the central reaches of the Rio Cuieiras which is a tributary on the left bank of the Rio Negro about 70 km upstream from Manaus. The lake is situated 36 km in a straight line from the mouth of the Rio Cuieiras on the right bank 2 km downstream from the mouth of the Rio Branquinho. It is separated from the river by a wide sand bank which is covered at high water (water depth 7,5 m). There is, however, a low water connection with the river via a small canal. The lake is completely surrounded by undisturbed igapó and is almost circular with a diameter of 0,1 km and a maximum water depth of 11,5 m. Even at high water it could be seen that an inflow existed. Since the Rio Cuieiras reaches a depth of 9 m, it can be assumed that the lake does not dry out completely at low water, i.e. it is a perennial water body. Data collected on 19.7.1971 characterise the lake and neighbouring waters as being typical black water, whose pH and conductivity values are comparable with those of Lago Tupé (Table 6).

Table 6: Limnological data for Lago do Cuieiras and Rio Cuieiras.

	Lago do Cuieiras		Rio Cuieiras
	0 m	11 m	0 m
Temperature	25,6°C	24,8°C	24,8°C
pH	4,45	4,40	4,50
μS_{20}	7,60	8,30	7,30
mg O ₂ /l	1,84	0,17	-
Secchi transparency	2,60 m		2,10 m

The lake was obviously stratified at the time of investigation as can be seen by the almost complete lack of oxygen in the water layers near the bottom. The sediment consisted of light brown mud with a sieve residue composed of fine and broken up leaf material and a few undestroyed leaves. This made up about one-quarter of the grab volume, and in appearance was reminiscent of sawdust.

The benthic fauna of the three grab samples collected consisted of living Ostracoda only, with an abundance of 15 individuals/m² and a biomass of 0,003 g/m². Lago Cuieiras together with Lago Caiuê, which is considered next, have the poorest benthic fauna, both in quality and quantity, of all the Central Amazon lakes which were investigated.

For comparison it is worth noting some zoobenthos data from the Rio Cuieiras itself, collected on 15.10.1971. The sampling site was about 2 km downstream on the left bank of the river on a smooth sandy shore in a current of moderate strength. The river was about 50 m wide. The shore vegetation consisted of a narrow band of igapó which passed into gently rising terra firme forest.

The data obtained from the middle of the river were: Secchi transparency 2,0 m; surface temperature 24,9°C; pH 4,65; conductivity 7,1 μS_{20} . Samples were collected along a transverse profile in water depths of 1,5 2,5 3,5 and 4,0 m. The content of coarse detritus, leaves, twigs, branches etc. decreased sharply from the shore to the middle of the river. The sediment in the two deepest samples was pure sand. Table 7 shows that in terms of % composition, the zoobenthos is hardly distinguishable from the

littoral zoobenthos of a black water lake (e.g. Lago Tupé). The Chironomidae are dominant, making up 48% of the total abundance. Towards the centre of the river there is a rapid qualitative and quantitative decrease in the benthic fauna so that on the river bed there were virtually no animals.

Table 7: Abundance and biomass values of the zoobenthos from the middle course of the Rio Cuieiras.

Ind./m ² (g/m ²)	Depth	1,5 m	2,5 m	3,5 m	4,5 m
Oligochaeta	311 (0,053)	-	-	-	-
Hirudinea	89 (0,177)	-	-	-	-
Acari	44 (-)	44 (-)	-	-	-
Odonata	44 (0,142)	-	-	-	-
Trichoptera	44 (-)	-	-	44 (0,098)	-
Heteroptera	1820 (0,386)	178 (0,060)	-	-	-
Ephemeroptera	89 (0,120)	-	-	-	-
Chaoboridae	-	44 (0,031)	-	-	-
Chironomidae	2797 (0,275)	311 (0,053)	-	-	-
Ceratopogonidae	44 (0,009)	-	-	-	-
total	5282 (1,163)	577 (0,145)	44 (0,098)	-	-

5.2. Lago Caiuê

This lake is on the left bank of the Rio Canumã, about 40 km from its mouth in the Paraná Urariá, which itself flows into the Rio Madeira on the right bank. The Rio Canumã is, like the neighbouring Rio Abacaxis, Rio Maués or the Rio Tapajós, a "river lake" in its lower reaches (SIOLI 1968), or a "ria lake" in the geomorphological sense. Lago Tupé, as has already been discussed, is a small ria lake. Lago Caiuê shows the same physiography. At the time of sampling (27.6.1971) it had a maximum width of 0,1 km, a maximum depth of 11,5 m and its inflow ran up into the terra firme for about 5 km. The banks were lined with a narrow band of igapó with adjoining high forest. The Secchi transparency was 2,70 m in the lake middle, pH was 5,9 and conductivity was 6,2 μS_{20} . Oxygen concentration could unfortunately not be determined. However, the absence of bottom fauna from all three samples in the central part of the lake indicates that there is very little oxygen near the bottom. The light brown soft sediments with relatively high proportions of sand and black unbroken leaves were similar to those of Lago Tupé.

5.3. Lago "Rio Preto da Eva" and Lago Jarí.

Finally there is a brief consideration of two lakes which were investigated limnologically by MARLIER (1965, 1967) and from which there are data on the benthos. I have not investigated these lakes myself.

The Rio Preto da Eva is the first large river to flow into the Amazon River after its confluence with the Rio Negro. The lower course forms a ria lake 30-40 km long which is joined to the Amazon River by a várzea canal (Paraná) of almost the same length. In contrast to Marlier's opinion, it seems to me that white water affects at least the lower part of

the lake for part of the year. The data presented here suggest no such influence but the position of the sampling stations is not known. However, it is clear that the lake is not a typical black water one since the Secchi transparency is too high (2,70-3,50 m) and the conductivity value given for April is extremely low ($3,9 \mu S_{20}$ at 0 m). Lago "Rio Preto da Eva" presumably has a larger rainwater input than, say, Lago Tupé; also, unlike Lago Tupé its waters are not in contact with a black water river and there is therefore no exchange. Thirdly, the Rio Preto da Eva flows through the lake for much of the year and the depths are well supplied with oxygen. In January and February the oxygen concentrations at 9 m are 4,06 and 6,21 mg/l respectively; stratification occurs only during the high water phase in waters where the depth exceeds 10 m, with accompanying oxygen deficiency near the bottom.

The main feature of these data is that the benthic fauna is qualitatively richer than, and has a different structure to, that of Lago Tupé. It is similar in composition to the fauna of some mixed water várzea lakes, with Oligochaeta and Tanypodinae larvae being dominant.

The same holds for Lago Jarí on the lower Rio Purús (MARLIER 1967). This lake is about 45 km long and is also not a typical black water lake; the conductivity at 0 and 5 m on 26.3. was only $2,7 \mu S_{20}$, a value close to that for the pure rain water of the region.

The ten samples of profundal fauna taken from the lake showed that Oligochaeta and Tanypodinae larvae are also dominant here. Chaoboridae larvae and Ostracoda are far less numerous both in the profundal fauna of this lake and in that of Lago "Rio Preto da Eva", unlike in Lago Tupé where they are dominant. As already mentioned the benthic fauna of these two lakes differs qualitatively from that of Lago Tupé partly because of differences in the nature of the water and also because the oxygen supply during the year is better in the bottom waters of the two lakes. However, it is possible that in the years when the deep water layers of Lago Tupé are better supplied with oxygen than in the high-water years 1971/72 the profundal zoocenose shows more group diversity and resembles those of Lago Jarí and Lago "Rio Preto da Eva" in qualitative composition.

6. Summary

Lago Tupé is a black water "ria lake". It is connected with the Rio Negro throughout the year and shows similarly large fluctuations in water level, amounting to nearly 8 m in 1971. The exceptionally high minimum water level of the one-year sampling period implied that there was thermal stratification in the lake throughout the year; because of this the oxygen content of the bottom water layers did not exceed 0,6 mg/l, and H_2S formed in the hypolimnion during the period of decreasing water level. These unfavourable external conditions led to the development of a qualitatively and, to a lesser extent, quantitatively poor benthic fauna in the lake centre. Dominant were Chaoboridae larvae (192 individuals/ m^2 over the year) and Ostracoda (457 individuals/ m^2 over the year); the Acari were sub-dominant (70 individuals/ m^2 over the year), and Nematoda were also present (10 individuals/ m^2 over the year). The mean annual biomass was $0.136 g/m^2$. The corresponding patterns of abundance and biomass were also determined for the year.

The benthic fauna of the littoral zone was investigated during the phases of low and rising water levels, also at a locally fixed sampling station. The characteristic littoral fauna appears only during the low water phase (November to January) when Chironomidae larvae are dominant with an abundance of 43-74 %. The rest of the fauna consists of many groups with low relative abundances. When the wa-

ter level begins to rise the qualitative composition alters completely within a few weeks, Chaoboridae larvae and Ostracoda becoming dominant. Apart from the absence of Acari the resulting zoocenose is qualitatively identical with the profundal zoocenose. It is conceivable that some of the true littoral species migrate at rising water to the neighbouring inundated forest (igapó), and move back again when the water level falls. The rhythmic faunal movements between profundal, littoral and igapó zones, caused by the large water level fluctuations, are schematically represented.

Biomass values were also determined in the littoral zone. The values for both this and abundance were much higher than in the lake centre at any given time.

The feeding habits of the individual taxa of profundal and littoral zoocenoses were examined. The Ostracoda are the detritophages of the profundal zoocenose; they are fed on by the zoophagous Acari and to a certain extent by the chaoborid larvae. In the true littoral zone the phytophages feed on blue green algae and diatoms growing on firm substrates; these are absent from both igapó and profundal zone. The fungi, which are an important food source in the igapó, play a lesser role in the littoral. The larvae of the Tanypodinae are the zoophages of the true littoral zone.

Finally, comparable studies of the zoobenthos of other black water lakes are discussed; these lend support to the inferences from Lago Tupé i.e. the profundal zone of the black water lakes has qualitatively and quantitatively the poorest benthic fauna of all lacustrine biotopes in the Central Amazon.

7. Resumo

O Lago Tupé é um "lago de ria" de água preta. Durante todo o ano está em conexão com o Rio Negro inferior, e segue as grandes oscilações de nível deste, que em 1971 atingiram quase 8 m. A queda extremamente grande do nível d'água inferior durante o período de investigação de um ano condicionou uma estratificação circunmanal que não permitiu aos teores de O_2 das camadas d'água junto ao fundo se elevarem acima de 0,6 mg/l, e que levou a uma formação de H_2S no hipolimnion. Em dependência destes exofatores desfavoráveis, desenvolveu-se uma fauna bentônica qualitativamente, e de forma abrangida também quantitativamente pobre na porção central do lago. Constitui-se das larvas de Chaoboridae (192 ind./ m^2 . ano) e Ostracoda (457 ind./ m^2 . ano), assim como dos grupos subdominantes Acari (70 ind./ m^2 . ano) e Nematoda (10 ind./ m^2 . ano). A biomassa média perfaz $0,136 g/m^2$. O ciclo anual de abundância e biomassa foi determinado.

Também a fauna bentônica litoral foi investigada em um local de coleta fixo durante a fase de água baixa e enchente. A fauna litoral característica estabelece-se apenas durante a água baixa de novembro a janeiro. Neste tempo dominam as larvas de Chironomidae com uma parcela de abundância de 43-74 %, à qual se junta uma fauna restante relativamente rica em grupos com abundâncias relativas baixas. Com o início da enchente, a composição qualitativa da fauna modifica-se totalmente através da ocorrência dominante das larvas de Chaoboridae e Ostracoda. A zoocenose estabelecida é qualitativamente idêntica à zoocenose de fundo, exceto quanto à falta dos Acari. Com a subida das águas pode ser verificada a probabilidade da existência de uma migração à mata de inundação vizinha, o igapó, para uma parte das espécies genuinamente litorais, enquanto com a descida das águas o movimento de migração tem sentido inverso. Um esquema visualiza as relações rítmicas das faunas entre as zonas profundal, litoral e de igapó ocasionadas pelas grandes oscilações do nível d'água.

Além dos valores de abundância do litoral também foram determinados os valores de biomassa. Ambos os parâmetros são claramente mais elevados do que os da porção central do lago, ao mesmo tempo. Tanto na zoocenose profundal como na litoral fazem-se considerações sobre o modo de alimentação dos diferentes taxons. A componente detritófaga da fauna profundal são os Ostracoda, dos quais se alimentam os Acari zoófagos, em parte provavelmente também as larvas de Chaoboridae. A biocenose litoral genuína dispõe de fontes de alimento para taxons fitófagos sob forma de tapetes de Cianofíceas e Diatomáceas sobre substrato sólido, que faltam nos biótopos vizinhos, as zonas de igapó e profundal. Os fungos, utilizados predominantemente no igapó, desempenham um papel quantitativamente menor no litoral. A principal componente zoófaga na zona litoral genuína é representada pelas larvas de Tanypodinae.

Finalizando, fazem-se considerações comparando investigações sobre o zoobentos de outros lagos

de água preta. Com isto constatou-se a idéia adquirida no Lago Tupé de que a zona profunda dos lagos de água preta apresenta qualitativa-se quantitativamente a fauna mais pobre de todos os biótopos lacustres da Amazônia Central.

(Tradução por Dr. Reimar Schaden).

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